Effects of ovulation rate and fetal number on fertility in twin-producing cattle

S. E. Echternkamp, R. A. Cushman, M. F. Allan, R. M. Thallman and K. E. Gregory

J Anim Sci 2007.85:3228-3238.
doi: 10.2527/jas.2007-0209 originally published online Jun 25, 2007;

Effects of ovulation rate and fetal number on fertility in twin-producing cattle[1,2]

S. E. Echternkamp,[3] R. A. Cushman, M. F. Allan, R. M. Thallman, and K. E. Gregory[4]

USDA-ARS, US Meat Animal Research Center, Clay Center, NE 68933

ABSTRACT: Effects of ovulation rate and of fetal number and distribution within the uterus on pregnancy rate and fetal survival were evaluated in nulliparous (n = 1,331) and parous (n = 3,517) cattle selected for twinning. Cattle were divided into a spring (70 d) and fall (60 d) breeding season and bred by a combination of AI and natural service. Ovulation rate, pregnancy status, and fetal number and distribution were determined by transrectal, real-time ultrasonography of the uterus and both ovaries at the end of the breeding season. Pregnancy was reconfirmed by rectal palpation at 75 to 135 d of gestation. For heifers and cows combined, ovulation rate increased ($P < 0.01$) from 1.46 ± 0.4 in 1994 to 1.89 ± 0.4 in 2004; number of calves per parturition increased ($P < 0.01$) from 1.34 ± 0.3 to 1.56 ± 0.3, respectively, which included an increase in triplet and quadruplet ovulations and triplet births. Bilateral twin ovulations yielded proportionately more ($P < 0.01$) twin births than unilateral twin ovulations. Ovulation rate was greater ($P < 0.01$) in the fall than spring breeding season. Pregnancy rate at ultrasound diagnosis did not differ among females with 1, 2, or 3 ovulations (89.1 ± 0.7, 91.2 ± 0.7, or 91.5 ± 2.8%, respectively), but rates at calving decreased ($P < 0.01$) with increasing ovulation rate (85.1 ± 0.6, 82.7 ± 0.6, or 64.2 ± 2.7%, respectively). Pregnancy rate was less ($P < 0.01$) after twin or triplet births than single births. For dams birthing twins or triplets, pregnancy rate was less in the fall vs. spring, but rates were similar between seasons for dams with a single birth (type of birth × season, $P < 0.05$). Cows ≤ 50 d postpartum had a decreased ($P < 0.01$) pregnancy rate compared with cows > 60 d, regardless of type of birth. Maintenance of pregnancy to term differed ($P < 0.01$) among females diagnosed with 1, 2, or 3 fetuses (95.7 ± 0.6, 87.8 ± 0.8, and 54.9 ± 2.3%, respectively). The reduced survival of twin and triplet fetuses in heifers had occurred ($P < 0.01$) by d 75 to 135 of gestation, and fetal losses were greater ($P < 0.01$) for unilateral than bilateral twins or triplets, whereas loss of twin or triplet fetuses in cows occurred later in gestation, and losses were not affected by uterine location. Thus, increased calf production from selecting for increased ovulation rate in beef cattle is tempered by increased fetal mortality, partially associated with the crowding of 2 or 3 fetuses within 1 uterine horn, especially in heifers.

Key words: cattle, fertility, fetal development, ovulation rate, twins, uterine capacity

J. Anim. Sci. 2007. 85:3228–3238
doi:10.2527/jas.2007-0209

INTRODUCTION

Cattle are primarily monovulatory, and the frequency of fraternal twin or multiple births is low. However, the frequency of twinning can be increased by hormone therapy (Echternkamp, 1992), embryo transfer (Anderson et al., 1979), or long-term genetic selection (Gregory et al., 1990; Echternkamp and Gregory, 2002). Results from such studies indicated that bovine females had the uterine capacity to support 2 fetuses, but the efficiency for supporting multiple fetuses diminished with increasing fetal numbers. Observations from FSH-treated cattle indicated maximal uterine capacity to be 3 fetuses within 1 uterine horn or a total of 5 fetuses per uterus; above these numbers, cows aborted at about 40 d of gestation (Echternkamp, 1992).

Unique to cattle is the anastomosis of the choronic blood vessels and the sharing of a common blood supply between twin or multiple fetuses (Echternkamp, 1999); thus, death of a fetus within this shared placental unit

[1]Mention of names are necessary to report factually on available data; however, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by the USDA implies no approval of the product to the exclusion of others that may also be suitable.

[2]Appreciation is expressed to Darrell Light for data analysis; to Gordon Hays, Michael Wilford, Loyal Clang, Doug Felber, and Arnold Svoboda for cattle operations and technical assistance; and to Linda Parnell for manuscript preparation.

[3]Corresponding author: Sherrill.Echternkamp@ars.usda.gov

[4]Deceased.

Received April 11, 2007.

Accepted June 21, 2007.

results in death of the other fetus(es), increasing fetal mortality for twin pregnancies. Natural or induced twin or multiple ovulations can occur on either the left or right ovary or both ovaries. Because migration of embryos between uterine horns is rare in cattle (Scanlon, 1972), bovine embryos implant in the uterine horn adjacent to the ovary from which the oocyte originated (Echternkamp, 1992). Preliminary results indicated that pregnancy rates in cattle were initially increased by twin ovulations (Echternkamp et al., 1990), but rates were reduced later in gestation by increased fetal mortality for twins (Anderson et al., 1982). However, information as to the effects of uterine crowding on development of twins and triplets is limited for cattle.

The objective of the current study was to assess the effects of ovulation rate and of fetal number and distribution within the uterus on fertility and on fetal survival and development in cattle.

MATERIALS AND METHODS

Animals and Experimental Design

Experimental design and procedures employed in this study were approved by the US Meat Animal Research Center (**USMARC**) Animal Care and Use Committee. The reported data were collected from 1994 to 2004 and included 1,331 nulliparous and 3,517 parous records from females in the Twinner population at USMARC. Age of the parous cows ranged from 3 to 11 yr. The Twinner population is composed of females selected for 4 to 5 generations for the production of twin births, utilizing repeated measurements of ovulation rate, individual animal EBV for twinning, and sires progeny-proven for twinning (Echternkamp et al., 1990; Gregory et al., 1990; Van Vleck et al., 1991). Selection protocols, management procedures, and breed composition have been reported previously (Gregory et al., 1990, 1996; Echternkamp and Gregory, 2002). Size of the Twinner herd was reduced from 750 to 300 breeding females from 1997 to 1998 primarily by culling females with the lowest EBV for twinning.

Approximately equal numbers of females comprised the spring and fall herds. Females in the spring herd were bred from late May to early August (70 d) and in the fall herd from late October to late December (60 d). Females with the greatest EBV for twinning (approximately one-third of the females) were bred by AI for 21 d to sires progeny-proven for twinning, followed by 50 (spring) or 40 (fall) d of natural service to individual young Twinner bulls to be progeny tested; cows received AI 12 h after estrus. The remaining two-thirds of the females were bred naturally to young, Twinner bulls to be progeny tested in individual-sire breeding pastures (25 females/sire) for the total breeding season. Because of the measurement of ovulation rate in all yearling heifers (Echternkamp et al., 1990), heifers were bred to calve first at 2.5 yr of age.

During the breeding seasons, the cattle were provided ad libitum access to grass pasture, which was supplemented with a diet of 70% corn silage and 30% alfalfa haylage (DM basis) during the fall breeding season. Dams gestating, birthing, and nursing a single were fed a diet of 70% haylage and 30% corn silage supplemented with alfalfa hay ad libitum pre- and postpartum until the beginning of breeding. Females diagnosed with twins or triplets were fed a high-energy diet (80% corn silage, 17.5% high moisture corn, and 2.5% protein supplement, DM basis) beginning an average of 70 (spring) or 50 (fall) d before the beginning of the calving season. Dams nursing twins were also fed this high-energy diet postpartum. Diets were fed to achieve a BCS of 5 to 6 on a schedule of 1 to 9 (NRC, 1996) during the pre- and postpartum periods. For triplet births with 3 live calves, 1 calf was cross-fostered to another dam.

Ovulation Rate Measurement and Pregnancy Diagnosis

Number of corpora lutea (**CL**) on the right and left ovary and number and distribution of fetuses between the uterine horns were determined by real-time ultrasonography (Echternkamp and Gregory, 1999). Examinations were performed transrectally by scanning the uterus and both ovaries with a 3.5-MHz convex-array probe (Aloka, Corometrics Medical Systems, Wallingford, CT). Ultrasound measurements were conducted primarily by 1 technician proficient in CL and fetal measurements, but a second technician conducted some measurements from 1994 to 1999. All females were examined about 70 d after the beginning of the spring and fall breeding seasons and within 5 d after the end of the breeding season. Females < 40 d of gestation or nonpregnant at the first examination were reexamined 35 to 40 d later. Thus, the ovulation rates measured were for the estrous cycle of conception in pregnant females or for the last estrous cycle of breeding in nonpregnant females. At the second ultrasound examination, ovulation rate was measured only in the newly diagnosed pregnant females, and rates were in excellent agreement between the first and second measurement. Pregnancy was reconfirmed by rectal palpation of the uterus from 75 to 135 d of gestation. Females failing to conceive or to maintain the pregnancy to term were assigned a numerical value of zero for type of birth.

Data Analysis

Data were analyzed by ANOVA using PROC MIXED (SAS Inst. Inc., Cary, NC). Ovulation rate and fertility data were analyzed separately for nulliparous heifers and parous cows (≥3 yr of age); cow was included as a random effect in the analysis of data for parous cows. Because of the reduced number of phenotypic records for cows > 6 yr of age, records were combined with those for 6-yr-old cows. Initial models included all possible 2-way interactions, but only the significant ($P \leq 0.05$) interactions were included in the final analysis. Effects

Table 1. Factors affecting ovulation rate in heifers and in cows ≥3 yr of age[1]

	Heifers		Cows	
Item	n	CL,[2] n	n	CL,[2] n
Year				
1994	85	1.44 ± 0.08[abe]	223	1.53 ± 0.04[a]
1995	100	1.36 ± 0.06[a]	272	1.48 ± 0.04[af]
1996	88	1.48 ± 0.06[abe]	205	1.59 ± 0.05[abg]
1997	118	1.50 ± 0.05[abe]	197	1.63 ± 0.04[bg]
1998	38	1.72 ± 0.09[bcfg]	149	1.77 ± 0.05[cd]
1999	56	1.77 ± 0.08[c]	122	1.79 ± 0.05[cd]
2000	77	1.71 ± 0.06[c]	224	1.75 ± 0.04[bdh]
2001	81	1.66 ± 0.07[bcg]	218	1.77 ± 0.04[cd]
2002	85	1.86 ± 0.06[cf]	216	1.75 ± 0.04[bdh]
2003	64	1.76 ± 0.07[c]	220	1.82 ± 0.04[cd]
2004	79	1.79 ± 0.06[c]	202	1.86 ± 0.04[cdi]
Season				
Spring	383	1.64 ± 0.03	1,191	1.59 ± 0.02[a]
Fall	488	1.64 ± 0.03	1,057	1.82 ± 0.02[b]
Type of birth[3]				
Nonpregnant			511	1.61 ± 0.03[a]
Single			998	1.63 ± 0.02[a]
Twins			694	1.70 ± 0.02[be]
Triplets			45	1.88 ± 0.08[bf]

[a–d]Within an item, means (±SEM) without a common superscript differ ($P < 0.01$).

[e–i]Within an item, means (±SEM) without a common superscript differ ($P < 0.05$).

[1]Ovulation rate [number of corpora lutea (CL)] was measured by ultrasonography 40 to 70 d after breeding by a single technician.

[2]Ovulation rate records were analyzed separately for nulliparous heifers and for primiparous and multiparous cows.

[3]Type of birth at preceding parturition; nonpregnant cows failed to conceive in the preceding breeding season.

of season (spring vs. fall) and year (1994 to 2004) and their interaction on ovulation rate were evaluated separately for nulliparous heifers and parous cows; the model for parous cows also included animal age, preceding type of birth, and their interactions. Length of the postpartum interval did not affect ovulation rate in parous cows and was excluded from the final statistical model. Changes in ovulation and twinning rate in parous cows with time (yr) were also assessed by regression analysis. Analyses reported in Tables 1 and 2 utilized ovulation rate measurements performed by only the primary ultrasound technician. Effects of type of ovulation (i.e., number and ovarian location of the CL), year, season, and animal age on number of calves born per female exposed to AI or bulls or per parturition were analyzed for nulliparous and parous females combined. Effects of type of ovulation, year, season, age (parous only), and preceding type of birth (parous only) on percentage of females pregnant at ultrasound diagnosis or at projected term were analyzed for nulliparous heifers and parous cows separately; this analysis included ovulation rate measurements by both technicians. Only the interaction of year × age at ultrasound diagnosis was significant and was included in the final analysis.

The effect of postpartum interval on percentage of dams pregnant at ultrasound or palpation diagnosis or at term was evaluated in only dams birthing a single calf or twins. Postpartum interval was defined as the number of days from parturition to the first day of the breeding season, and cows were categorized into 6 time intervals: ≤50, 51 to 60, 61 to 70, 71 to 80, 81 to 90, and >90 d postpartum. The statistical model also included preceding type of birth, age of dam, year, and season.

Analysis of factors affecting maintenance of pregnancy included fetal status, year, and season. Preceding type of birth and age of dam did not affect fetal survival in parous dams and were deleted from the final model. Fetal status was classified by the number and distribution of fetuses between the left and right uterine horns: single left, single right, unilateral twins left, unilateral twins right, bilateral twins, unilateral triplets, and bilateral triplets; data for the small number of unilateral triplets in the left or right horn were combined. For females calving, records having a discrepancy between number of diagnosed fetuses and number of calves born were deleted from the analysis of pregnancy maintenance. The effect of ovulation rate on the distribution of type of birth was evaluated within classifications by χ^2 analysis. Comparisons of fertility between contemporary heifer and cow groups were analyzed by χ^2 analysis.

RESULTS

Ovulation Rate and its Relationship to Number of Calves Born

Ovulation rate (Table 1) increased ($P < 0.01$) by chronological year. The overall rate of increase in ovulation rate from 1994 to 2004 for all female progeny was 0.034 CL/yr. Ovulation rate for parous cows was greater ($P < 0.01$) in the fall than spring breeding season, whereas ovulation rate for nulliparous heifers did not differ between seasons. Dams birthing twins or triplets had a greater ($P < 0.01$) ovulation rate postpartum than dams birthing a single calf or nonpregnant females (i.e., failed to conceive in previous breeding season). Ovulation rate was not affected by age of parous cows.

Consistent with ovulation rate, the largest increase ($P < 0.01$) among years in number of calves born per female exposed or calving (Table 2) occurred from 1997 to 1998. The overall rate of increase in number of calves per parturition from 1994 to 2004 was 0.025 calves/yr, whereas number of calves born per female exposed to breeding only had a transient increase ($P < 0.05$) in 1998. Number of calves born per female exposed or calving was greater ($P < 0.01$) for females with twin or triplet ovulations vs. a single ovulation. Also, the number of calves born per parturition (Table 2) was further increased ($P < 0.01$) with triplet vs. twin ovulations; however, the number born per female exposed did not differ between triplet and twin ovulations. In addition, bilateral twin ovulations yielded proportionately more calves than unilateral twin ovulations. Distribution of single or unilateral twin ovulations between the left and right ovary, or bilateral vs. unilateral triplet

Table 2. Factors affecting number of calves born per female exposed or calving

Item	Females, n	Calves/females exposed[1]	Females, n	Calves/parturition[2]
Year				
1994	308	1.15 ± 0.08[e]	251	1.37 ± 0.04[a]
1995	372	1.12 ± 0.06[a]	311	1.33 ± 0.04[a]
1996	293	1.07 ± 0.06[a]	247	1.32 ± 0.05[a]
1997	315	1.06 ± 0.05[a]	253	1.33 ± 0.04[a]
1998	187	1.30 ± 0.09[bf]	157	1.55 ± 0.05[be]
1999	178	1.16 ± 0.08[e]	144	1.47 ± 0.05[bf]
2000	301	1.19 ± 0.06	237	1.52 ± 0.04[b]
2001	299	1.13 ± 0.07[a]	231	1.53 ± 0.04[b]
2002	301	1.15 ± 0.06[e]	229	1.55 ± 0.04[be]
2003	284	1.15 ± 0.07[e]	232	1.48 ± 0.04[b]
2004	281	1.14 ± 0.06[a]	214	1.55 ± 0.04[be]
Season				
Spring	1,574	1.10 ± 0.03[a]	1,294	1.39 ± 0.03[a]
Fall	1,545	1.18 ± 0.03[b]	1,212	1.50 ± 0.03[b]
Type of ovulation				
1 Left	569	0.84 ± 0.03[a]	475	1.03 ± 0.03[a]
1 Right	726	0.82 ± 0.03[a]	594	1.03 ± 0.03[a]
2 Left	329	1.31 ± 0.04[be]	264	1.67 ± 0.03[b]
2 Right	605	1.33 ± 0.03[b]	486	1.68 ± 0.03[b]
2 Bilateral	723	1.40 ± 0.03[bf]	583	1.76 ± 0.03[c]
3 Unilateral	37	1.26 ± 0.12[b]	20	2.20 ± 0.03[d]
3 Bilateral	130	1.40 ± 0.06[b]	84	2.19 ± 0.03[d]
Age, yr				
2	871	1.17 ± 0.03[a]		
3	730	1.18 ± 0.03[a]		
4	554	1.18 ± 0.03[a]		
5	359	1.10 ± 0.03[ab]		
≥6	605	1.01 ± 0.03[b]		

[a–d]Within an item, means (±SEM) without a common superscript differ ($P < 0.01$).
[e,f]Within an item, means (±SEM) without a common superscript differ ($P < 0.05$).
[1]Number of calves born per number of females in the breeding herd.
[2]Number of calves born per number of females calving (parturition).

ovulations, did not affect number of calves born. For females calving, the ratio of calves born:CL number was 1.03 for single, 0.86 for twin, and 0.73 for triplet ovulations (Table 2). Consistent with ovulation rate, number of calves per dam was greater ($P < 0.01$) in the fall than spring calving season. Also, number of calves per female exposed was decreased ($P < 0.01$) in females ≥ 6 yr of age compared with the younger age groups; number of calves per parturition was not affected by age of dam.

The relationship between ovulation rate and subsequent type of birth is reported in Table 3. Bilateral twin ovulations yielded a greater ($P < 0.05$) percentage of twin births and fewer ($P < 0.05$) single births than unilateral twin ovulations. Distribution of the fetuses between the left and right uterine horn reflected the increased frequency of single and twin ovulations on the right ovary. Because of the small number of observations for triplet ovulations, the percentage of births being triplet, twin, or single did not differ between bilateral and unilateral triplet ovulations.

Pregnancy Rate

Factors affecting the percentage of females pregnant at 40 to 70 d of gestation (ultrasound pregnancy diagnosis), 75 to 135 d of gestation (palpation pregnancy diagnosis), or at calving were evaluated separately for nulliparous heifers and parous cows. Also, data were analyzed with records for single or twin ovulations on the left and right ovaries evaluated separately (Table 4) or the 2 ovaries combined (Figure 1). The effect of length of the postpartum interval on pregnancy rate was assessed in only dams birthing a single or twins.

Heifers. The percentage of nulliparous heifers pregnant at ultrasound diagnosis and at calving (Table 4) was influenced by number and distribution of ovulations between the left and right ovary. At ultrasound diagnosis, heifers with a single ovulation on the right ovary had a lower pregnancy rate than heifers with unilateral twin ovulations on the right ovary ($P < 0.01$), bilateral twin ovulations ($P < 0.01$), or bilateral triplet ovulations ($P < 0.05$). When data for the left and right ovary were combined, heifers with a single ovulation had a lower ($P < 0.01$) pregnancy rate at ultrasound diagnosis than heifers with twin ovulations (Figure 1). In contrast, pregnancy rates at calving were similar for left or right single ovulations and bilateral twin ovulations. Also, pregnancy rate at calving was greater for heifers with a left single ovulation than with left ($P < 0.01$) or right ($P < 0.05$) unilateral twin or triplet ($P <$

Table 3. Effects of ovulation rate and distribution of ovulations between ovaries on type of birth

Ovulation rate	CL location[2]	n	Type of birth,[1] % Single	Twins	Triplets
1	Left	475	97.5[a]	2.5	
	Right	594	97.1[a]	2.9	
2	Left	264	36.4[bd]	63.6[d]	
	Right	486	35.4[bd]	64.6[d]	
	Bilateral	583	25.6[be]	74.4[e]	
3	Unilateral	20	5.0	65.0	30.0
	Bilateral	84	19.0	40.5	40.5

[a,b]Percentages within a column without a common superscript differ ($P < 0.01$).
[d,e]Percentages within a column without a common superscript differ ($P < 0.05$).
[1]Percentage of pregnant females within an ovulatory subgroup producing single, twin, or triplet births. Ovulation rate was determined by ultrasonography at 40 to 70 d of gestation.
[2]Distribution of ovulations [corpora lutea (CL)] between the left and right ovary at conception.

0.01) ovulations and greater for right single ovulations than for left unilateral twin ovulations ($P < 0.05$), unilateral triplet ovulations ($P < 0.01$), or bilateral triplet ovulations ($P < 0.05$). Overall, heifers with unilateral twin or triplet ovulations had a lower ($P < 0.05$) pregnancy rate at calving than single or bilateral twin or triplet ovulations (Figure 1). Heifers with unilateral triplet ovulations had the lowest ($P < 0.01$) pregnancy rate, differing from heifers with single ($P < 0.01$), twin ($P < 0.01$), or bilateral triplet ($P < 0.05$) ovulations (Figure 1). Pregnancy rate for bilateral triplet ovulations was similar to unilateral twin ovulations but differed ($P < 0.05$) from single or bilateral twin ovulations. Pregnancy rate did not differ between spring- and fall-bred heifers or among the 11 yr evaluated.

Cows: Ovulation Rate. The association between ovulation rate (Table 4) and pregnancy rate at ultrasound diagnosis included a greater ($P < 0.05$) pregnancy rate for cows with unilateral twin ovulations on the left ovary compared with a single ovulation or bilateral twin ovulations. Pregnancy rate for triplet ovulations did not differ from single or twin ovulations (Figure 1). At calving, pregnancy rates did not differ between cows with single and twin ovulations, but cows with bilateral ($P < 0.01$) or unilateral ($P < 0.10$) triplet ovulations had a lower calving rate compared with single or twin ovulations. Pregnancy was reduced ($P < 0.01$) in cows ≥ 6 yr of age at ultrasound diagnosis, but the reduction was not significant in all years (year × age of dam; $P < 0.05$); pregnancy rate was similar among all ages at

Table 4. Factors affecting pregnancy rate in nulliparous heifers and parous cows at ultrasound pregnancy diagnosis and at calving[1]

Item	Heifers n	Ultrasound, %	Calving, %	Cows n	Ultrasound, %	Calving, %
Type of ovulation[2]						
1 Left	295	92.5 ± 1.6	88.8 ± 1.5[ae]	682	87.2 ± 1.9[e]	82.5 ± 1.0[a]
1 Right	324	88.9 ± 1.5[ae]	85.5 ± 1.5[abeh]	925	86.5 ± 1.8[e]	82.3 ± 0.9[a]
2 Left	145	92.4 ± 2.3	77.9 ± 2.9[bfg]	330	93.9 ± 2.5[f]	83.3 ± 1.8[a]
2 Right	221	95.9 ± 1.8[b]	81.0 ± 2.3[abfgh]	657	91.5 ± 2.0	81.3 ± 1.3[a]
2 Bilateral	290	94.5 ± 1.6[b]	85.5 ± 2.1[abeh]	767	88.1 ± 2.0[e]	79.4 ± 1.3[a]
3 Unilateral	17	94.1 ± 6.0	52.9 ± 7.5[c]	29	86.2 ± 6.5	62.1 ± 5.5
3 Bilateral	39	97.4 ± 4.0[f]	71.8 ± 4.9[bcg]	127	92.1 ± 3.5	63.7 ± 2.7[b]
Age, yr						
3				1,094	90.7 ± 1.8[a]	83.1 ± 1.0
4				861	89.2 ± 1.9[a]	81.0 ± 0.9
5				592	90.9 ± 2.0[a]	80.8 ± 1.8
≥6				970	84.2 ± 1.8[b]	77.8 ± 1.8
Season						
Spring	581	94.0 ± 1.0	82.4 ± 1.2	1,948	88.8 ± 0.5	82.4 ± 0.7[e]
Fall	750	91.9 ± 0.9	84.9 ± 1.2	1,569	88.9 ± 0.6	78.7 ± 0.7[f]

[a–c]Means within a column and item without a common superscript differ ($P < 0.01$).
[e–g]Means within a column and item without a common superscript differ ($P < 0.05$).
[1]Percentage of females (means ± SEM) in the breeding herd pregnant at ultrasound pregnancy diagnosis (d 40 to 70 of gestation) or at calving. Pregnancy records were analyzed separately for nulliparous heifers and for primiparous and multiparous cows and for the 2 evaluation times within age groups.
[2]Number and location of ovulations on the left and right ovary at conception or at last breeding. Ovulation rate measurements are the combined data for 2 technicians.

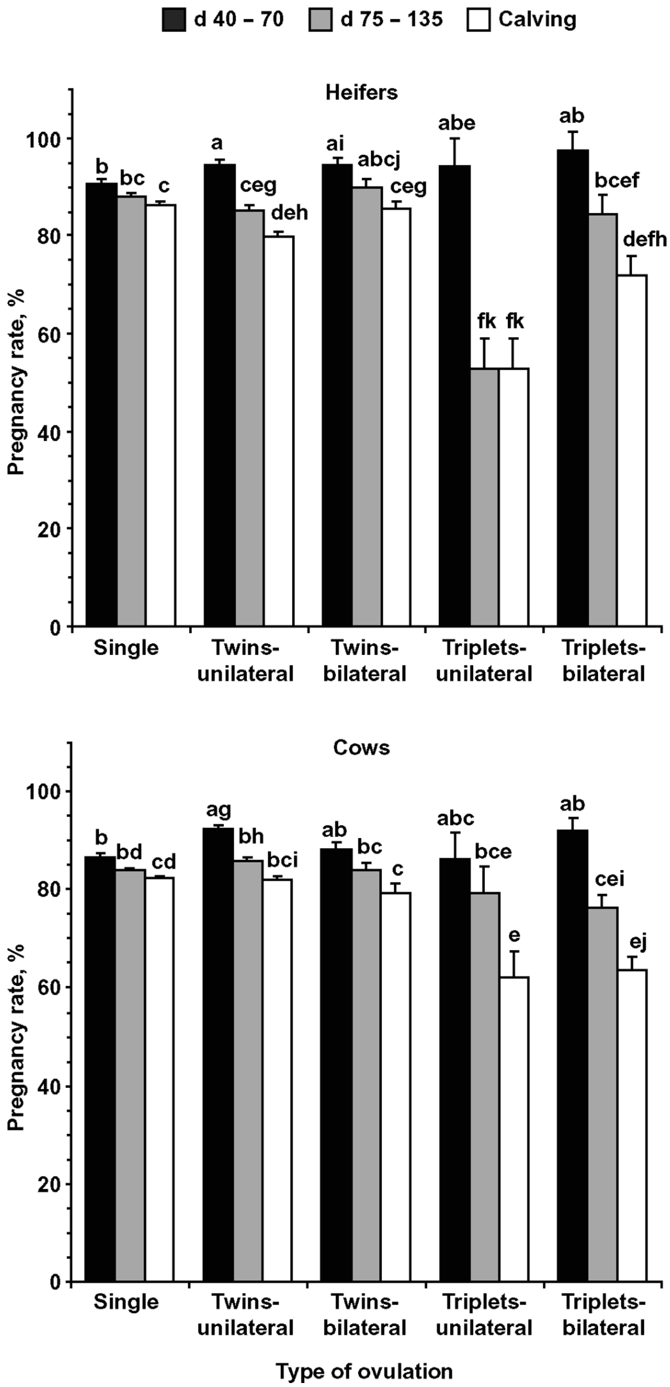

Figure 1. Comparison of pregnancy rates at (■) d 40 to 70 of gestation, (■) d 75 to 135 of gestation, or (□) at calving for nulliparous heifers or parous cows with single, unilateral twin, bilateral twin, unilateral triplet, or bilateral triplet ovulations. [a–f]Means within a parity group without a common superscript differ ($P < 0.01$). [g–k]Means within a parity group without a common superscript differ ($P < 0.05$).

calving. In contrast, the percentage of cows pregnant was similar between seasons at ultrasound diagnosis, but it was reduced ($P < 0.05$) in the fall at calving. Pregnancy rates decreased ($P < 0.01$) by year from 1996 to 2004 at both stages of gestation.

Cows: Type of Birth. In general, pregnancy rate was less ($P < 0.01$) after twin or triplet births than single births (Table 5). Rates at ultrasound or palpation diagnosis did not differ between postpartum dams birthing twins or triplets but were less ($P < 0.05$) after triplets at calving. Contributing to the lower pregnancy rate after twin births was their lower pregnancy rate in the fall vs. spring (type of birth × season; $P < 0.05$). Except at ultrasound diagnosis (i.e., single vs. twin; $P < 0.05$), pregnancy rates did not differ among the 3 birth groups in the spring, but, in the fall, rates were lower for dams birthing twins or triplets compared with singles at all 3 stages of gestation. Preceding type of birth did not affect pregnancy rate in primiparous (3-yr-old) dams, but dams ≥ 4 yr of age birthing twins or ≥ 5 yr of age birthing triplets had lower pregnancy rates at both ultrasound diagnoses and at calving than dams birthing a single (type of birth × age of dam; $P < 0.05$). Age of dam did not affect pregnancy rate after a single birth.

Percentage of dams establishing and sustaining pregnancy (Table 5) also differed between seasons among years (year × season; $P < 0.05$); rates were greater in the spring vs. fall in 1994, 1995, 1997, and 1998, but not in the other 7 yr, at all 3 stages of gestation. A comparison of pregnancy rates among years showed a general decrease ($P < 0.01$) in rates from 1996 to 2004, but rates did vary among years. The overall range in percentage of females pregnant at ultrasound diagnosis, palpation diagnosis, and calving ranged from 89.7 ± 1.9, 86.4 ± 2.0, and 84.8 ± 5.0%, respectively, in 1996 to 75.0 ± 2.7, 69.6 ± 2.8, and 65.8 ± 4.4%, respectively, in 2004 ($P < 0.01$).

Postpartum Interval. Number of days from parturition to beginning of breeding season also influenced pregnancy rate when evaluated for only dams with single or twin births (Table 6). The primary effect of postpartum interval was a lower pregnancy rate in cows < 50 d ($P < 0.01$) or 51 to 60 d ($P < 0.05$) postpartum compared with intervals of 71 to 80 d or longer. Again, pregnancy rate was reduced in the fall compared with the spring for dams birthing twins but did not differ between seasons for dams birthing a single (type of birth × season; $P < 0.05$). Dams ≥ 6 yr of age had a lower ($P < 0.05$) pregnancy rate at both ultrasound and palpation diagnosis, and dams ≥ 5 yr of age and birthing twins had a lower pregnancy rate at calving than dams birthing a single (type of birth × age; $P < 0.05$). Pregnancy rates differed between spring and fall breeding in some years as noted above (season × year; $P < 0.01$). Differences in percentage calving between dams birthing a single calf vs. twins were about 8% fewer for dams with twins in most years, but the birth groups differed by 0.2% in 1999, 13.2% in 1995, and 15.0% in 1997 (type of birth × year; $P < 0.05$).

Maintenance of Pregnancy

For evaluation of factors affecting the maintenance of pregnancy in nulliparous heifers or parous cows ges-

Table 5. Effects of previous type of birth, age of dam, year, and season on pregnancy rate in postpartum dams ≥3 yr of age

Item	Dams, n	Ultrasound,[1] %	Palpation,[1] %	Calving,[1] %
Type of birth[2] (TOB)				
Single	2,098	87.3 ± 1.0[af]	83.7 ± 1.2[a]	81.6 ± 1.4[a]
Twins	1,301	79.2 ± 1.1[b]	75.7 ± 1.2[b]	72.0 ± 1.6[bf]
Triplets	66	78.0 ± 4.6[abg]	68.6 ± 5.2[b]	57.6 ± 1.8[bg]
Age, yr × TOB				
3 Single	677	87.7 ± 1.5[ae]		82.1 ± 1.8[ag]
3 Twins	400	82.7 ± 1.9[abg]		77.5 ± 2.2[abg]
3 Triplets	18	100.0 ± 8.9[abfgh]		72.2 ± 10.3[acdghi]
4 Single	499	88.1 ± 1.7[af]		83.2 ± 2.0[ag]
4 Twins	329	81.6 ± 2.1[agi]		72.0 ± 2.4[bc]
4 Triplets	17	84.7 ± 9.2[acg]		71.3 ± 11.0[acgi]
5 Single	317	88.6 ± 2.2[af]		81.1 ± 2.5[abg]
5 Twins	241	77.8 ± 2.4[bci]		69.3 ± 2.8[cdhi]
5 Triplets	12	73.9 ± 10.9[ac]		50.0 ± 14.3[acehj]
≥6 Single	605	84.7 ± 1.6[a]		79.8 ± 2.0[abdg]
≥6 Twins	331	74.6 ± 2.1[cdi]		67.4 ± 2.4[c]
≥6 Triplets	19	54.3 ± 8.7[dj]		36.8 ± 10.2[ej]
Season × TOB				
Spring single	1,176	87.3 ± 1.3[af]	85.0 ± 1.5[a]	82.8 ± 1.5[a]
Spring twins	639	82.8 ± 1.5[acg]	80.0 ± 1.7[a]	78.6 ± 1.8[a]
Spring triplets	30	84.9 ± 7.0[ab]	80.0 ± 7.9[acf]	66.7 ± 8.2[ab]
Fall single	922	87.2 ± 1.4[af]	82.0 ± 1.7[a]	79.9 ± 1.8[a]
Fall twins	662	75.5 ± 1.5[b]	71.0 ± 1.7[bg]	65.7 ± 1.7[b]
Fall triplets	36	71.0 ± 6.5[bc]	58.3 ± 7.7[bch]	50.0 ± 8.4[b]

[a–e]Means within a column and item without a common superscript differ ($P < 0.01$).
[f–j]Means within a column and item without a common superscript differ ($P < 0.05$).
[1]Percentage (means ± SEM) of cows pregnant at ultrasound pregnancy diagnosis (d 40 to 70 of gestation), palpation pregnancy diagnosis (d 75 to 135 of gestation), or calving. Analyses included records for dams with and without ovulation rate information.
[2]Type of birth at preceding parturition.

Table 6. Factors affecting pregnancy rate in postpartum dams after a single or twin birth

Item	Dams, n	Ultrasound,[1] %	Palpation,[1] %	Calving,[1] %
Postpartum interval,[2] d				
<50	464	77.6 ± 1.8[ad]	72.8 ± 1.9[ad]	69.1 ± 2.0[ad]
51–60	383	83.2 ± 1.9[abe]	78.4 ± 2.1[abe]	76.2 ± 2.2[abe]
61–70	844	85.3 ± 1.3[b]	81.2 ± 1.5[bceg]	79.9 ± 1.5[bc]
71–80	1,003	88.6 ± 1.2[c]	85.0 ± 1.3[cf]	81.5 ± 1.4[c]
81–90	549	85.5 ± 1.6[bc]	82.2 ± 1.8[bcfg]	79.4 ± 1.8[bc]
91+	156	88.3 ± 3.0[bcf]	84.3 ± 3.2[bcf]	81.9 ± 3.4[c]
Age, yr				
3	1,077	84.6 ± 1.2[abd]	80.4 ± 1.3[abd]	78.6 ± 1.4[a]
4	828	85.5 ± 1.4[a]	81.2 ± 1.5[a]	77.7 ± 1.6[a]
5	558	84.4 ± 1.6[abd]	80.3 ± 1.8[abd]	74.8 ± 1.8[ab]
≥6	936	80.6 ± 1.3[be]	76.0 ± 1.4[bc]	72.1 ± 1.5[b]
Type of birth (TOB)				
Single	2,098	88.4 ± 1.0[a]	84.1 ± 1.1[a]	80.3 ± 1.1[a]
Twins	1,301	79.2 ± 1.1[b]	74.8 ± 1.2[b]	70.5 ± 1.2[b]
Season				
Spring	1,814	87.6 ± 1.1[a]	84.3 ± 1.2[a]	81.8 ± 1.2[a]
Fall	1,585	83.9 ± 1.1[b]	78.7 ± 1.2[b]	73.8 ± 1.3[b]
Season × TOB				
Spring single	1,176	88.7 ± 1.4[a]		80.8 ± 1.5[a]
Spring twins	639	82.6 ± 1.5[b]		76.8 ± 1.7[b]
Fall single	922	88.0 ± 1.5[a]		79.6 ± 1.7[ab]
Fall twins	662	75.8 ± 1.5[c]		64.1 ± 1.7[c]

[a–c]Means within a column and item without a common superscript differ ($P < 0.01$).
[d–g]Means within a column and item without a common superscript differ ($P < 0.05$).
[1]Percentage (means ± SEM) of cows pregnant at ultrasound (d 40 to 70 of gestation), palpation pregnancy diagnosis (d 75 to 135 of gestation), or at calving.
[2]Postpartum interval was the number of days from parturition to the first day of the breeding season.

tating 1, 2, or 3 fetuses, fetal number and their distribution between the left and right uterine horn were determined by ultrasonography from d 40 to 70 of gestation. Pregnancy status was reassessed by rectal palpation of the uterus from d 75 to 135 of gestation and by number of calves born at expected time of calving. Percentage of both heifers and cows maintaining their pregnancy to term was affected by season and fetal number and by whether twin and triplet fetuses were within the same uterine horn or in separate uterine horns. However, maintenance of pregnancy was similar for fetuses in the left vs. right uterine horn, irrespective of whether they were single, unilateral twin, or unilateral triplet pregnancies. Percentage calving was greater ($P < 0.05$) in the fall vs. spring for heifers and vice versa for cows.

Heifers. The percentage of heifers maintaining their pregnancy to either palpation diagnosis or to term was greater for heifers diagnosed with a single fetus compared with twin ($P < 0.05$) or triplet ($P < 0.01$) fetuses. For heifers with a single fetus, pregnancy rate decreased 2% between ultrasound and palpation diagnosis and an additional 1 to 2% between palpation and calving. Pregnancy rates were similar for nulliparous heifers and parous cows gestating a single fetus.

Maintenance of pregnancy for bilateral twins was similar to a single fetus at palpation but was reduced ($P < 0.01$) at calving, whereas heifers diagnosed with unilateral twins had lower ($P < 0.01$) pregnancy rates at both palpation and calving than heifers with a single. Also, heifers with bilateral twins maintained a greater pregnancy rate to both palpation and calving compared with unilateral twins in either the left ($P < 0.05$) or right ($P < 0.01$) uterine horn. Maintenance of a bilateral twin pregnancy to either palpation or calving was similar for heifers and cows, but fewer heifers maintained a unilateral twin pregnancy to term.

Pregnancy losses, especially at palpation, were greatest for heifers with a unilateral triplet pregnancy, differing from a bilateral triplet pregnancy at palpation ($P < 0.05$) and at calving ($P < 0.01$) and from ($P < 0.01$) the other fetal groups at both evaluation times. Heifers with bilateral triplets had a lower pregnancy rate than heifers with bilateral twins ($P < 0.05$) or a single ($P < 0.01$) at both evaluation times. The incidence of unilateral triplet pregnancies at calving was similar between heifers and cows.

Cows. Pregnancy loss from ultrasound to palpation diagnosis (Table 7) for cows gestating a single fetus was 3 to 4% with an additional 1 to 2% loss between palpation and calving. Maintenance of pregnancy to palpation was similar for cows gestating a single fetus, bilateral twins, or right unilateral twins, but cows with left unilateral twins had a lower pregnancy rate than cows with a left ($P < 0.05$) or right ($P < 0.01$) single. Pregnancy maintenance to palpation in cows with unilateral triplets did not differ from cows with unilateral twins or bilateral triplets, but it was less ($P < 0.05$) than for cows with a single fetus or bilateral twins.

Maintenance of pregnancy to calving differed ($P < 0.01$) among the 3 fetal groups (Table 7), maintenance of twins being less ($P < 0.01$) than for singles but greater ($P < 0.01$) than for triplets. However, the distribution of twin fetuses bilaterally vs. unilaterally or the distribution of single or twin fetuses in the left vs. right uterine horns did not affect maintenance of pregnancy to term. Calving rate was reduced ($P < 0.05$) for unilateral compared with bilateral triplet pregnancies.

DISCUSSION

Long-term genetic selection of cattle for increased ovulation rate has sustained an increasing ovulation rate and an associated 3%-per-year increase in the frequency of fraternal twins. The large increase in ovulation and twinning rate from 1997 to 1998 was primarily the consequence of reducing herd size from 750 to 300 breeding females by culling females with the lowest EBV for twinning. Also contributing to the increase in ovulation rate in recent years has been an increasing frequency of triplet and quadruplet ovulations, which has increased the frequency of triplet births and recently produced a set of quadruplet female calves (Bennett et al., 2006). Just as in monovulatory cattle, the right ovary of Twinner cattle has more follicular activity and ovulations than the left ovary (Echternkamp et al., 1990; Echternkamp and Gregory, 2002; Cushman et al., 2005); thus, a greater proportion of the twin fetuses were gestated unilaterally in the right vs. left uterine horn, and the percentage of bilateral twins was < 50%. Previously observed postpubertal increases in ovulation rate in the Twinner population (Echternkamp et al., 1990; Cushman et al., 2005) likely account for the greater ovulation rates in the older nulliparous and parous females in the current study compared with those reported for yearling Twinner heifers (Cushman et al., 2005). However, the yearly linear increase in ovulation rate reported for the yearling Twinner heifers was similar to the increase found in the nulliparous and parous females in the current study (0.026 vs. 0.034 CL/yr, respectively), especially when adjusted for the effect of age.

As anticipated, number of calves born per parturition increased with ovulation rate. However, in those females maintaining their pregnancy to term, the proportion of calves born per ovulation (calf:CL ratio) was 0.86 for twin ovulations and 0.73 for triplet ovulations rather than 1.0. These calf:CL ratios in pregnant females with twin or triplet ovulations are similar to reported conception rates (0.80) to 1 insemination in monovulatory beef cattle (Maurer and Chenault, 1983), implicating that ovulation failure, abnormal oocyte quality, or embryonic anomalies are major contributors to reproductive losses in beef cattle and likely have a greater influence on fertility than maternal uterine influences. An exception to this interpretation is the increased fetal mortality in nulliparous heifers with 2 or 3 fetuses in 1 uterine horn. An earlier evaluation (Echternkamp et al., 1990)

Table 7. Effects of fetal number and uterine location, season, and year on maintenance of pregnancy from ultrasound diagnosis to palpation diagnosis or to calving[1]

	Heifers			Cows		
Item	n	Palpation, %	Calving, %	n	Palpation, %	Calving, %
Number and location of fetuses[2]						
1 Left	362	98.1 ± 1.2[a]	96.6 ± 1.5[a]	827	96.1 ± 0.8[abe]	95.4 ± 1.0[a]
1 Right	381	98.2 ± 1.2[a]	97.1 ± 1.5[a]	1,018	97.0 ± 0.7[ae]	95.3 ± 0.9[a]
2 Left	97	88.4 ± 2.3[bceg]	82.5 ± 2.9[bce]	225	91.5 ± 1.5[bfg]	88.5 ± 1.8[b]
2 Right	156	87.5 ± 1.8[b]	80.0 ± 2.3[c]	440	93.6 ± 1.1[ab]	88.1 ± 1.3[b]
2 Bilateral	187	94.2 ± 1.7[acf]	89.2 ± 2.1[bf]	471	95.3 ± 1.1[abeg]	90.7 ± 1.3[b]
3 Unilateral	14	45.5 ± 6.1[d]	45.5 ± 7.5[dg]	25	83.3 ± 4.5[abcf]	58.3 ± 5.5[ce]
3 Bilateral	33	81.0 ± 4.0[bcg]	71.4 ± 4.9[cde]	101	82.9 ± 2.1[c]	65.7 ± 2.7[cf]
Season						
Spring	545	92.3 ± 1.0	86.7 ± 1.2[a]	1,718	95.5 ± 0.5	93.2 ± 0.7[e]
Fall	685	95.1 ± 0.9	93.1 ± 1.2[b]	1,386	94.1 ± 0.6	91.4 ± 0.7[f]

[a–d]Means within a column without a common superscript differ ($P < 0.01$).
[e–g]Means within a column without a common superscript differ ($P < 0.05$).
[1]Data expressed as percentage (means ± SEM) of females maintaining pregnancy from ultrasound pregnancy diagnosis (d 40 to 70 of gestation) until palpation pregnancy diagnosis (d 75 to 135 of gestation) or until calving.
[2]Fetal number and location within the uterus was determined by ultrasonography from d 40 to 70 of gestation and was confirmed by number of calves born at calving.

of the effect of ovulation rate on conception rate provided similar results and showed that conception losses within the first 21 d after breeding were independent of ovulation rate.

Pregnancy losses after d 40 to 70 of gestation were nominal (i.e., 3 to 4%) for both nulliparous heifers and parous cows gestating a single fetus in either the left or right uterine horn and were similar to those reported previously for monovulatory cattle (Hawk, 1979; Beal et al., 1992). The correlated increase in twinning rate with increasing ovulation rate indicates that most of the females in this population have the uterine capacity to gestate twin fetuses to term. Because the foundation Twinner animals were selected for twinning rate, and twinning rate is included in the computed twinning EBV, Twinner females may possess superior uterine capacity and support for twin and triplet pregnancies compared with unselected females. Existence of differences in uterine capacity among females could be tested by reciprocal transfer of embryos between Twinner females and contemporary females unselected for twinning. However, evaluations of the influence of fetal numbers and their distribution between the left and right uterine horn did reveal a negative effect of increasing fetal number on the maintenance of pregnancy to term as well as possible differences in uterine capacity between nulliparous and parous females. In nulliparous heifers, pregnancy losses at d 75 to 135 of gestation were 2- to 3-fold greater for unilateral twin pregnancies compared with bilateral twin pregnancies, and this difference persisted to calving. In contrast, pregnancy maintenance did not differ between unilateral and bilateral twin pregnancies in parous cows, but survival was reduced for both unilateral and bilateral twin fetuses compared with singles. Thus, the percentage of females maintaining a bilateral twin pregnancy to term was similar for heifers and cows, whereas maintenance of the unilateral twin pregnancy was already compromised in heifers by d 75 to 135 of gestation. A similar difference was observed between Hereford heifers and cows with unilateral vs. bilateral twins produced by embryo transfer (Anderson et al., 1979). Thus, uterine capacity in heifers appears to be restrictive for the development of 2 fetuses in 1 uterine horn. Differences in maternal support for singles or unilateral twins were not detected between the left and right uterine horn.

Pregnancy losses were substantially greater for triplet pregnancies compared with single or twin pregnancies for both heifers and cows. Greater than 50% of the unilateral triplet pregnancies in heifers were already aborted by d 75 to 135 of gestation compared with losses of 19 and 29% for bilateral triplet pregnancies at palpation and calving, respectively. Although the abortion of unilateral triplets occurred earlier in gestation in heifers than in cows, the percentage of females maintaining triplet pregnancies to term was similar for nulliparous heifers and parous cows. Thus, the possible adverse effect of uterine crowding or some other maternal inadequacy on development of triplet fetuses, especially unilateral triplet pregnancies, was apparent in both nulliparous heifers and parous cows but occurred earlier in gestation in heifers.

A model developed by Bennett et al. (1998) for the distribution of single, twin, and triplet or greater-order births in cattle with increasing ovulation rate showed good agreement ($P = 0.31$) with the actual litter size distribution found in the USMARC Twinner herd from 1998 to 2005 (Bennett et al., 2006). At birth, 940 single, 823 twin, and 69 triplet or quadruplet parturitions were obtained compared with model predictions of 948.8 single, 804.0 twin, and 79.3 triplet or quadruplet parturitions. Although not significantly different, predicted numbers of triplet births were greater than those observed. The prediction model did not include any uterine capacity or fetal location effects, except for 6 or more fetuses, but these results may provide further evidence of uterine restriction with 3 or more fetuses.

Contributing to the increased fetal abortion for twin and triplet pregnancies in cattle is the greater frequency (>95%; Gregory et al., 1996) of in utero fusion of the chorionic membranes and anastomosis of the chorionic blood vessels between twin or triplet fetuses in cattle than in other species (Echternkamp, 1999). Death of a fetus within the fused placental unit caused death of the other fetus(es) and termination of the pregnancy (Echternkamp, 1992), thus increasing the probability of fetal mortality and abortion with increasing fetal numbers.

The production of twins is repeatable in the USMARC Twinner population (Gregory et al., 1997), and, thus, assessment of the effect of ovulation rate or preceding type of birth on rebreeding performance was confounded by dams with twins having an increased ovulation rate at the ensuing breeding season. Percentage of females pregnant at ultrasound diagnosis was similar or greater for females with twin or triplet ovulations, the increased number of oocytes providing an increased opportunity for conception. However, because of the increased fetal mortality with triplet pregnancies, percentage of females calving was reduced with triplet ovulations. Thus, the number of calves born per female exposed to breeding did not differ between twin and triplet ovulations. Conversely, twin and triplet births tended to reduce rebreeding performance compared with single births. This trend for decreased pregnancy rates after twin or triplet births was partially the consequence of interactions between type of birth and season or age of dam. For dams with a preceding twin or triplet birth, but not a single birth, pregnancy rate was reduced in the fall compared with the spring and at ≥ 6 yr of age compared with younger ages. However, the seasonal difference in pregnancy rate was not statistically significant after the reduction in herd size in 1998. The lower pregnancy rate in the fall and in older dams after a twin birth has been a reoccurring trend in this population (Echternkamp et al., 1990; Echternkamp and Gregory, 1999). Because twinning is repeatable, cows with a twin birth are more likely to conceive twins or triplets at the subsequent breeding. Thus, the decreased pregnancy rate in fall-bred cows is associated with the increased ovulation rate in the fall and the repeatability of twinning and the lower conceptus survival for twin or triplet pregnancies. Conversely, the diet of the fall-bred cows was supplemented with a high-energy concentrate during the postpartum and breeding periods, and BCS were comparable or increased for cows in the fall vs. spring herd, reducing the possibility of negative effects of nutrition on conception in the fall. Similarly, complications (e.g., dystocia, retained placenta, and physiological stress) associated with twin or multiple births (Guerra-Martinez et al., 1990; Echternkamp and Gregory, 1999) may compromise reproductive longevity of twin-producing cattle; thus, the decreased pregnancy rate for dams ≥ 6 yr of age.

Shortening the postpartum anestrous period increases conception in postpartum beef cattle (Laster et al., 1973; Short et al., 1990); however, the postpartum anestrous period is generally longer for dams of twins (Turman et al., 1971; Guerra-Martinez et al., 1990). Because of the shorter gestation length for twin pregnancies and the rigid yearly breeding schedule for the Twinner population, dams producing twins or triplets at USMARC generally have a longer interval from parturition to the beginning of the breeding season. Thus, the negative effect of a longer postpartum anestrous period with twins on conception was minimized in the Twinner population.

Increased twinning in the fall vs. spring concurs with the greater ovulation rate in the fall season. The increased ovulation rate in the fall may be a consequence of a greater energy diet ("flushing" effect) for the diet of the fall herd was supplemented with a high energy concentrate during the breeding season compared with predominately grass pasture during the spring breeding season. Alternatively, seasonal differences in ovulation rate may be associated with increasing LH secretion in the fall months (Day et al., 1986). The increased ovulation rate in the fall has been observed previously (Echternkamp et al., 1990; Echternkamp and Gregory, 1999). Unfortunately, part of the potential production gain from an increased ovulation rate in the fall breeding season was compromised by reduced fertility in fall-bred cows birthing or conceiving twins or triplets.

In summary, the correlated increase in twinning rate with increasing ovulation rate indicates that most females in this population have the uterine capacity to gestate twin fetuses to term. However, greater pregnancy losses for unilateral vs. bilateral twin pregnancies in the nulliparous heifers infers that uterine capacity compromised fetal development in heifers with 2 or 3 fetuses in 1 uterine horn, which occurred by d 75 to 135 of gestation. Furthermore, the lower pre- and postnatal survival rate for triplets indicated that uterine capacity is limiting for triplets regardless of maternal age but occurs later in gestation in parous cows. Continued selection of cattle for an increasing frequency of twin ovulations has increased the frequency of triplet and quadruplet ovulations and, thus, triplet and quadruplets births. Because of increased fetal mortality and pregnancy losses associated with triplet pregnancies, it appears that little additional beneficial gains will be achieved from further increases in ovulation rate.

LITERATURE CITED

Anderson, G. B., R. H. BonDurant, and P. T. Cupps. 1982. Induction of twins in different breeds of cattle. J. Anim. Sci. 54:485–490.

Anderson, G. B., P. T. Cupps, and M. Drost. 1979. Induction of twins in cattle with bilateral and unilateral embryo transfer. J. Anim. Sci. 49:1037–1042.

Beal, W. E., R. C. Perry, and L. R. Corah. 1992. The use of ultrasound in monitoring reproductive physiology of beef cattle. J. Anim. Sci. 70:924–929.

Bennett, G. L., M. F. Allan, R. A. Cushman, and S. E. Echternkamp. 2006. Observed and predicted numbers of single, twin, and triplet births in a cattle population selected for increased twinning. J. Anim. Sci. 84(Suppl. 1):203. (Abstr.)

Bennett, G. L., S. E. Echternkamp, and K. E. Gregory. 1998. A model of litter size distribution in cattle. J. Anim. Sci. 76:1789–1793.

Cushman, R. A., M. F. Allan, G. D. Snowder, R. M. Thallman, and S. E. Echternkamp. 2005. Evaluation of ovulation rate and ovarian phenotype in pubertal heifers from a cattle population selected for increased ovulation rate. J. Anim. Sci. 83:1839–1844.

Day, M. L., K. Imakawa, P. L. Pennel, D. D. Zalesky, A. C. Clutter, R. J. Kittok, and J. E. Kinder. 1986. Influence of season and estradiol on secretion of luteinizing hormone in ovariectomized cows. Biol. Reprod. 35:549–553.

Echternkamp, S. E. 1992. Fetal development in cattle with multiple ovulations. J. Anim. Sci. 70:2309–2321.

Echternkamp, S. E. 1999. Freemartin. Pages 406–417 in Encyclopedia of Reproduction. Vol. 2. K. Knobil and J. Neill, ed. Acad. Press, San Diego, CA.

Echternkamp, S. E., and K. E. Gregory. 1999. Effects of twinning on gestation length, retained placenta, and dystocia. J. Anim. Sci. 77:39–47.

Echternkamp, S. E., and K. E. Gregory. 2002. Reproductive growth, feedlot and carcass traits of twin vs. single births in cattle. J. Anim. Sci. 80(E. Suppl. 2):E64–E73.

Echternkamp, S. E., K. E. Gregory, G. E. Dickerson, L. V. Cundiff, R. M. Koch, and L. D. Van Vleck. 1990. Twinning in cattle. II. Genetic and environmental effects on ovulation rate in puberal heifers and postpartum cows and the effects of ovulation rate on embryonic survival. J. Anim. Sci. 68:1877–1888.

Gregory, K. E., G. L. Bennett, L. D. Van Vleck, S. E. Echternkamp, and L. V. Cundiff. 1997. Genetic and environmental parameters for ovulation rate, twinning rate, and weight traits in a cattle population selected for twinning. J. Anim. Sci. 75:1213–1222.

Gregory, K. E., S. E. Echternkamp, and L. V. Cundiff. 1996. Effects of twinning on dystocia, calf survival, calf growth, carcass traits, and cow productivity. J. Anim. Sci. 74:1223–1233.

Gregory, K. E., S. E. Echternkamp, G. E. Dickerson, L. V. Cundiff, R. M. Koch, and L. D. Van Vleck. 1990. Twinning in cattle. I. Foundation animals and genetic and environmental effects on twinning rate. J. Anim. Sci. 68:1867–1876.

Guerra-Martinez, P., G. E. Dickerson, G. B. Anderson, and R. D. Green. 1990. Embryo-transfer twinning and performance efficiency in beef production. J. Anim. Sci. 68:4039–4050.

Hawk, H. 1979. Infertility in dairy cattle. Pages 19–29 in Beltsville Symp. Agric. Res. 3. Anim. Reprod. H. W. Hawk, ed. Allanheld, Osmon and Co., Montclair, NJ.

Laster, D. B., H. A. Glimp, and K. E. Gregory. 1973. Effects of early weaning on postpartum reproduction of cows. J. Anim. Sci. 36:734–740.

Maurer, R. R., and J. R. Chenault. 1983. Fertilization failure and embryonic mortality in parous and nonparous beef cattle. J. Anim. Sci. 56:1186–1189.

NRC. 1996. Page 35 in Nutrient Requirements of Beef Cattle. 7th rev. ed. Natl. Acad. Press, Washington, DC.

Scanlon, P. F. 1972. Frequency of transuterine migration of embryos in ewes and cows. J. Anim. Sci. 34:791–794.

Short, R. E., R. A. Bellows, R. B. Staigmiller, J. G. Berardinelli, and E. E. Custer. 1990. Physiological mechanisms controlling anestrus and infertility in postpartum beef cattle. J. Anim. Sci. 68:799–816.

Turman, E. J., D. B. Laster, R. E. Renbarger, and D. F. Stephens. 1971. Multiple births in beef cows treated with equine gonadotropin (PMS) and chorionic gonadotropin (HCG). J. Anim. Sci. 32:962–967.

Van Vleck, L. D., K. E. Gregory, and S. E. Echternkamp. 1991. Prediction of breeding values for twinning rate and ovulation rate with a multiple trait, repeated records animal model. J. Anim. Sci. 69:3959–3966.